Assessment of environmental and host dependent factors correlated with tick abundance on Komodo dragons

Tim S. Jessop[1,2], Joanna Sumner [3], Jeri Imansyah [4], Deni Purwandana [4], Aganto Seno [5], Achmad Ariefiandy [4] and Claudio Ciofi [6]

[1] Center for Conservation and Research of Endangered Species, Zoological Society of San Diego, Escondido Ca 92112, USA.

[2] Department of Wildlife Conservation and Science, Zoo's Victoria. PO BOX 74 Parkville VIC 3052, Australia.

[3] Museum Victoria, Carlton Gardens VIC, 3068, Australia.

[4] Komodo Dragon Species Survival Program Indonesia, Denpasar, Bali, Indonesia.

[5] Komodo National Park, Labuan Bajo, Flores, Indonesia

[6] Department of Animal Biology and Genetics, University of Florence, via Romana 17, 50125 Florence, Italy

ABSTRACT

In this study we assessed interactions among Komodo dragon *Varanus komodoensis* populations, individual Komodo dragons and two tick parasites *Amblyomma robinsoni* and *Aponomma komodoense* to assess variation in host-parasite aggregations. Prevalence of ticks was uniformly high (> 98%) but median tick abundance varied 3.52 fold among 9 host lizard populations. There was no evidence to suggest that average tick abundances were correlated with genetic similarities ($R_{m =}$ 0.133, P = 0.446) or geographic proximities (R_m = 0.175 P=0.303) among host populations. Temporal concordance in tick abundance was measured for host populations between two different years but not for the individual hosts within these populations. General linearized modelling indicated that ≈ 23% of host variation in tick abundance was positively correlated to a multivariate function incorporating lizard body size, body condition, their interactions, and habitat differences. The covariates of host population density and inbreeding coefficients, which are often associated with significant variation in parasite abundance, were not associated with variation in tick abundance on Komodo dragons. However, despite larger lizards generally harbouring more ticks, relative levels of ticks (controlling for host body mass differences) indicated that smaller individuals carried significantly higher tick abundances compared to larger lizards. There was no significant interaction between tick abundance and an individual host's growth rate. The major implications of our results indicated considerable variation in tick abundance across their host's range and that host body size is likely to be a significant determinant to what degree ticks impact the fitness of their hosts.

Key words: Key words: Host parasite dynamics, islands, *Varanus komodoensis*, Komodo dragons, ectoparasites, ticks.

Introduction

There is considerable evidence suggesting that ticks are aggregated across their host populations, with most individuals harbouring few parasites, but some individuals hosting many (see reviews by Shaw and Dobson 1995; Wilson *et al.* 2002). Furthermore, these distributions can represent predictable patterns of tick aggregation at both the individual and population level of the host. Understanding such patterns is valuable, as it reflects the competitive fitness dynamic between ticks and their hosts. Functionally, ticks exploit their hosts for nutrients and energy, whilst the host mounts immunological responses to reduce parasite recruitment and survival (Wikel and Bergman 1997; Cattadori *et al.*, 2005). Ticks can elicit both innate and specific acquired immune responses in the host, which impedes the tick's capacity to feed. The tick counteracts the host's immune response with immunosuppressive proteins (Wikel and Bergman 1997). This fitness dynamic is reflected in the prevalence and diversity of parasites and the degree of costs to the host.

In short, temporal and spatial variation in parasite-host dynamics can result in a continuum of costs to wildlife populations. Hence, some vertebrate populations are negatively affected by ticks whilst in other populations of the same species the effect of ticks appears to be minimal (i.e. hosts are locally adapted to ticks) (Fourie *et al.* 1992; Dunlap & Mathies 1993; Lampo and Bayliss 1996; McKilligan 1996; DelGiudice *et al.* 1997; Hudson *et al.* 1998).

Dramatic variation in parasite aggregations among individual hosts can arise due to multiple interactions among parasite, host and environmentally dependent factors (Shaw *et al.* 1998; Wilson *et al.* 2002). Hence the current distribution of parasites in individuals of a host species, and associated fitness costs is a reflection of the evolutionary and ecological dynamics of the host-parasite interactions. Some of the most predictable and hence non-random variation in parasite aggregation patterns is attributed to individual host variation in age, sex, body

condition, behaviour, immunogenetics and immunology (Anderson and May 1981; Zuk 1990; Wilson *et al.* 2002). External environmental factors can also influence patterns of parasite aggregations by limiting the rates of transmission of parasites among their hosts. For example, seasonal or habitat variables could alter the opportunity for hosts to acquire or transmit parasites (Wilson *et al.* 2002).

Variation in parasite aggregation exists not only among individuals but also among populations or demes of a host. For example, in archipelagos, where host/parasite populations may be distributed across several islands, evolutionary and ecological processes may differ and can greatly influence the interactions between hosts and parasites. Thus islands potentially offer study systems in which it is possible to separate ecological and evolutionary effects of host-parasite interactions by allowing for replicated evolutionary events between ecologically analogous, yet discrete islands (Fallon *et al.* 2003). Variation in parasite prevalence among island populations can arise because of unique genetic and ecological attributes of hosts or host-specific parasites. Fallon *et al.* (2003) suggested that, depending on the stability of these effects in space and time, parasite-host dynamics may either be repeated across islands, or vary between locations. Island area and habitat diversity are among the major factors influencing trophic processes that affect communities and have been recognised as important mediators of parasite-host dynamics (de Bellocq *et al.* 2002; Nieberding *et al.* 2006). Variation in the host environment, including the host-population density, the level of population inbreeding and the body condition of individuals in the host population may also influence host-parasite dynamics (Acevedo-Whitehouse *et al.* 2003; Spielman *et al.* 2004; Moller and Rozsa 2005). To date there have been few examinations of the dynamics between hosts and their tick ectoparasites among island populations (but see Whiteman *et al.* 2006).

In this study we examined multiple covariates commonly associated with predictable (i.e. non-random) patterns of ectoparasite aggregation in vertebrates. Specifically, we examined relationships among Komodo dragons *Varanus komodoensis* (Figure 1), a large carnivorous monitor lizard, and the abundance of two species of tick ectoparasites, *Amblyomma robinsoni* (Robinson, 1926; Figure 1) and *Aponomma komodoense* (Oudemans, 1929; Figure 2). Komodo dragons were studied at nine field sites on four adjacent island populations in the Lesser Sunda region of south-eastern Indonesia. This island system is of particular interest as it provides replication of environment (2 large versus 2 small islands) and, using previously reported genetic diversity estimates for the host species (Ciofi and Bruford 1999), provides different evolutionary histories among the islands, reflecting differing dispersal potential and levels of inbreeding.

Our first aim was to describe spatial and temporal variation in tick aggregations among Komodo dragon populations as indicated by the prevalence of infected hosts and the mean number of parasites per host population at each study site. Presumably, closely adjacent populations would share greater commonalities with respect to their genetic relatedness (maintained via gene flow) or through

environmental conditions structuring their habitats compared to more spatially disjunct populations. Thus we examined if either genetic divergence or geographic distance among populations was associated with any patterns of tick abundance. Further, we examined whether parasite abundance was variable over time on hosts. Understanding the temporal dynamics of parasite abundance is fundamentally important to understanding the epidemiological consequences of ticks on their hosts (Wilson *et al.* 2002).

Figure 1. An adult male Komodo dragon with ticks (*Amblyomma robinsoni*) imbedded at several places on its head including the sub-orbital area, behind the tympanum, and on the nape of the neck.

Figure 2. *Aponomma komodoense* ticks are endemic to the Komodo dragon. The ruler's scale is in millimeters.

The second aim of our study examined multiple environmental and host dependent variables that are expected to influence tick abundance on their lizard hosts. Variables for consideration included island area and habitat diversity. Both variables are among the major factors influencing trophic processes in island communities and have been recognised as important mediators of parasite-host dynamics (de Bellocq *et al.* 2002; Nieberding *et al.* 2006). We also considered that because individual hosts vary in their body condition (due to prey resource differences) and experience differences in population density (a numerical response to prey availability) and their respective population heterozygosity levels (i.e. inbreeding), these factors could be important covariates explaining differences in tick abundance on Komodo dragons (Acevedo-Whitehouse *et al.* 2003; Spielman *et al.* 2004; Moller and Rozsa 2005). Because parasites evolve more quickly than hosts, it is thought that genetically uniform hosts (i.e. from more inbred and/or small populations) are more susceptible to parasitism than genetically variable hosts (Moritz *et al.* 1991; Cassinello *et al.* 2001; Spielman *et al.* 2004). Hence we expected to find higher parasite abundances in the more inbred populations compared to the larger, more genetically variable populations. We also expected to find higher parasite abundances in populations with lower average body condition and higher population densities. Hence we expected variation in parasite abundance among Komodo dragons because of the unique genetic and ecological attributes of the hosts and the host-specific parasites. To understand the relationships between these multiple variables and their potential for predicting variation in tick abundance on Komodo dragons we used a multivariate modelling approach.

The third aim of this study was to assess scaling relationships between body size and individual host tick abundance by examining relative tick abundance (calculated as tick load / body mass to eliminate the effect of body size differences among individuals). Assessing relative tick load is very important in large bodied animals such as Komodo dragons, which exhibit ≈ 800 fold increase in mass through ontogeny. Given this huge range in host body size, relative tick abundance is likely to be a better measure of parasite cost to an individual. Differences in host-parasite relationships can reveal patterns of non-random parasite aggregations on individuals and are useful for inferring, at one level, how hosts might control their parasites through reduced exposure, increased innate resistance, acquired immunity, or a combination of these factors. Several conspicuous epidemiological patterns between host and parasite are noted and include age/size and sex biased dependencies of parasite aggregations (Wilson *et al.* 2002).

Our final aim was to assess if an individual varanid host's tick abundance was correlated with any fitness costs. Given that ticks feed directly on their host's blood there is the potential that energy/nutrient trade-offs may arise. This may cause impairment to other somatic or maintenance functions, including decreased somatic growth, which could lead to decreased host fitness (Wikelski 1999, Uller and Olsson 2004). In wild populations assessing parasite related fitness costs, particularly sub-lethal effects, can be difficult due to logistical and statistical problems (Woolhouse 1998), spatial variation in susceptibility or genetic variations between host populations (Cattadori *et al.* 2005). Nevertheless, significant non-random patterns of aggregations within and between populations may exist and can provide evidence that may help us to understand patterns in this host-parasite system.

Materials and Methods

Field sites and capture methods

Komodo dragons and their ticks were sampled at nine field sites on four islands in Komodo National Park in the Lesser Sunda region of south-eastern Indonesia (Figure 3). Studies were undertaken in 2003 and 2005. These islands encompass the extant distribution of this species within Komodo National Park and include populations from Komodo (393.4 km^2), Rinca (278.0 km^2), Gili Motang (10.3 km^2) and Nusa Kode (also referred to as Gili Dasami; 9.6 km^2). Within Komodo and Rinca, three and four sites per island, respectively, were selected to assess interactions between dragons and ticks, and included the valleys of Loh Sebita, Loh Lawi and Loh Wau on Komodo Island, and Loh Buaya, Loh Baru, Loh Tongker and Loh Dasami on Rinca Island (Fig. 1). On the small mountainous islands of Gili Motang and Nusa Kode, studies were confined to the coastal flats and adjacent hills representing approximately 20% of available island habitat.

Komodo dragons were captured using baited traps, nooses or by hand (smaller size classes only). In combination, these methods are extremely effective for capturing all size classes of Komodo dragons above yearlings, which are largely arboreal and rarely susceptible to these capture techniques. Following capture, dragons were restrained with rope and their mouths taped shut. Several morphological measurements were taken, including snout-to-vent length (SVL) and body mass. Dragons were permanently marked using passive integrated transponders (Trovan ID100a) inserted into the right hind leg.

Spatial and temporal variation in tick prevalence and abundance among host populations

Tick prevalence was calculated as the percentage of individuals on which there was at least one tick. Tick abundance for individual lizards was calculated by direct combined counts of *Amblyomma robinsoni* and *Aponomma komodoense* attached to the host's body (Auffenberg 1981; King and Green 1999). Both tick species are considered host specific as they have only been recorded on *Varanus komodoensis*, even in habitat where the Komodo dragon overlaps with its congener, *V. salvator* (Auffenberg 1981).

To assess temporal patterns in parasite load we recaptured host individuals in 2005 to compare tick loads between the 2003 and 2005 samples. Between these two events tick counts were performed at the same sites and conducted at same time of the year. To analyse spatial and temporal
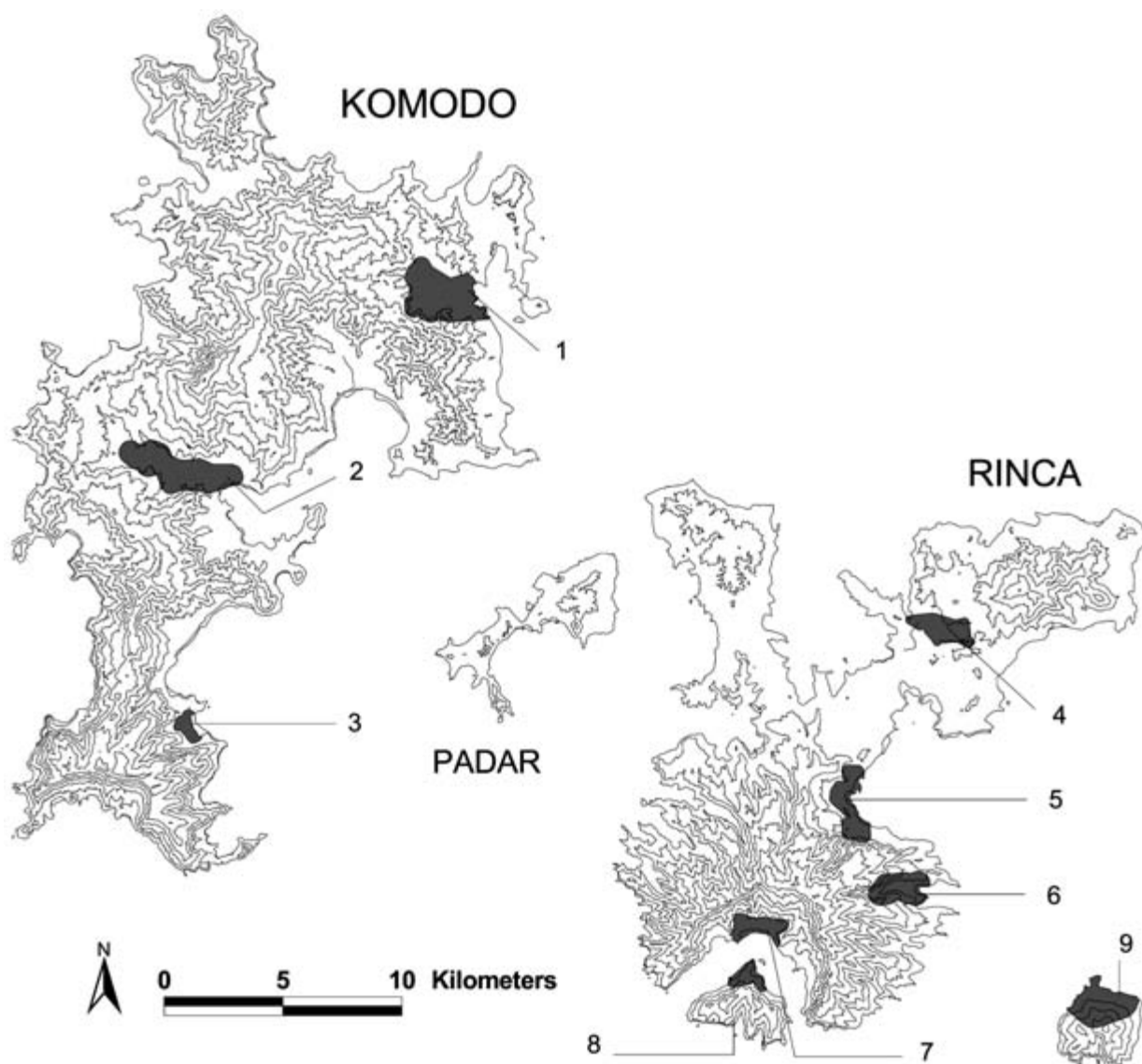
Figure 3. Map of Komodo National Park illustrating island study sites (grey areas) where data was collected. Within Komodo and Rinca, three and four sites, respectively, per island were selected to assess interactions between dragons and ticks. Included are the valleys of Loh Sebita (1), Loh Lawi (2) and Loh Wau (3) on Komodo Island, and Loh Buaya (4), Loh Baru (5), Loh Tongker (6) and Loh Dasami (7) on Rinca Island (Fig. 1). The two small mountainous islands of Nusa Kode (8) and Gili Motang (9) were also sampled.

variation in tick abundance among sample host populations we first used a one-way chi square test to assess frequency differences in the prevalence (number of infected hosts / total number of sampled hosts) of lizard hosts infected with ticks. To ascertain if mean tick abundance differed among host populations we used ANOVA on log $(x+1)$ transformed data. To analyse temporal variation in tick abundance between 2003 and 2005 we used paired t-tests to assess annual differences. In addition, we used regression analysis to determine whether individual host's tick abundances were correlated over time. The above analyses were conducted using SPSS 13 (SPSS Inc., USA).

To assess whether average tick abundance was structured by the genetic similarity or geographic proximity among host populations we used Mantel tests (with 10000 permutations) using the program XLSTAT (version 2006.5, Addinsoft, USA). These analyses evaluated the correlation between the dependent matrix (tick abundance) and the

two independent matrices: genetic differentiation (F_{st} values from Ciofi *et al.*, 2004) and geographic distance (calculated as the straight line distance among the centroid of each study site) among host populations. To construct a matrix for tick abundance, we calculated multidimensional Euclidean distance means (using SPSS 13, SPSS Inc., USA) of 8 pairwise distance values among each host population.

Assessing of environmental and host dependent factors associated with tick abundance.

We investigated multiple putative covariates across three levels of interactions, including: (1) broad scale environmental factors, (2) host population differences and (3) individual host differences, to assess whether these factors were significantly associated with parasite abundance on their lizard hosts. The factors we measured comprised:

a) Island area (km²): calculated from digital topographic maps using Arc View 3.1.

b) Site habitat composition: habitat scores were calculated by identifying vegetation communities along 150 m transects used for assessing deer pellet density (Jessop *et al.* 2006). Four main habitat types were present: (1) closed monsoon forest, (2) open deciduous forest, (3) savannah woodland, and (4) savannah grassland. For each transect a score was calculated according to the proportion of each vegetation type along the transect. These numbers were averaged for each site (20-47 transects), then for each island, to give an overall habitat score to describe each island within the context of this study. Scores closer to 1 indicated a wetter environment and more closed forest and scores closer to 4 indicate a drier more open habitat.

c) Host population inbreeding coefficients: Components of variance of allele frequencies calculated: a) for between individuals within populations and b) for between alleles within individuals (Weir and Cockerham 1984) were used to infer Wright's inbreeding coefficient F_{IS} using GENETIX 4.01 (Belkhir *et al.* 2000) to assess whether there was a relationship between mean log tick abundance per population and the level of population inbreeding at each of the nine study sites. Data for these estimates were drawn from previously published work on the population genetics of Komodo dragons (for methods refer to Ciofi 2002).

d) Host population density: calculated using an index based on catch per unit effort / km² using (CPUE / km²) such that population CPUE / km² = (no. of dragons captured at each field site / no. of trapping days conducted at each site in 2003).

e) Body condition: calculated using the regression equation of mass (natural log transformed) plotted against body length (using snout to vent length, natural log transformed). Transformation of data reduced the influence of changes in body shape during ontogeny and thus eliminated scaling differences.

f) Sampling month: given that sites were not sampled at the same time, but rather from March through to October, it was important to consider potential temporal variation as a covariate influencing tick abundance.

To assess if one or more of these variables (and their interactions) could predict variation in tick abundance on Komodo dragons we used a multivariate generalized linear modelling approach (GLM) conducted in the program R (http://www.r-project.org/). A generalized linear model differs from a general linear model in two major areas: first, the distribution of the dependent variable can be (explicitly) non-normal, and does not have to be continuous, i.e., it can be binomial, multinomial, or ordinal multinomial (contain information on ranks only), second, the dependent variable values are predicted from a linear combination of predictor variables, which are connected to the dependent variable via a link function.

To facilitate model development we used the following preliminary selection procedure based on assessing linear, quadratic and polynomial regressions to identify which variables were statistically significant at $P \leq 0.010$. Variables above this significance band were not included in the starting model for GLM. Effectively, we used a forward stepwise variable deletion process where we iteratively excluded variables and/or their interactions from the modelling process that either did not statistically contribute to explaining variation in tick abundance and those that were most heavily parameterized (i.e multivariate non-linear interactions). To produce the most parsimonious model (one indicating strongest support for the data) we used the Akaike Information Criterion (AIC), to compare the fit of models containing different numbers of variables.

Assessment of scaling relationships between tick abundance and host body size

To assess whether any scaling effect existed between Komodo dragon body size and tick abundance we calculated a relative measure of tick abundance that effectively eliminated the mass difference among individual hosts. We then estimated the relative body mass-tick abundance specific function using a generalized smoothing spline regression approach conducted using R. Smoothing spline regression uses the data to determine the underlying linear or nonlinear trend without assuming any specific functional form. Such an approach is valuable when there is no prior expectation or theory to suggest a particular functional equation to describe the relationship. A credible interval for the relationship is derived using Bayesian cross validation (Gu 2002).

Assessment of relationships between tick abundance and lizard fitness related traits

Growth: growth rate in dragons is size/age specific, thus, in order to eliminate the effect of body size on growth, growth was based on residual scores from a linear regression of annual growth increment on head length. Using head length as the axis of growth is preferred over snout-vent length, or total body length, as it has the lowest coefficient of variation (Jessop unpublished data).

Results

1) Spatial and temporal patterns in tick prevalence and abundance across host sampling sites.

A total of 238 Komodo dragons were captured and assessed for ticks across the nine field sites on four islands. Across these sites the prevalence of ticks was uniformly high, ranging from between 88.57 and 100.00 % of lizards carrying ticks (Table 1). Tick prevalence did not differ significantly among lizard populations on each island ($\chi^2_{1,8} = 0.72$, $P = 0.79$). Among the nine host populations there were significant differences in mean tick abundance ($F_{8,230} = 10.41$, $P < 0.001$), which ranged from 300.60 ± 135.00 ticks / lizard for the Sebita population on Komodo Island to a low of 26.5 ± 3.74 ticks / lizard for the Motang Island population. The mean estimate of the Sebita population tick abundance was highly skewed

Table 1. Tick parameters on Komodo dragons sampled from 9 populations on four islands in Komodo National Park, Indonesia. Host sample size is represented by *N*. Post-hoc tests indicate homogenous host populations with respect to their tick abundance log (x+1).

Island	Population	Prevalence	Mean abundance	Std. Error	Median	Range	N (hosts)	Post-hoc subgroups
Komodo	Lawi	100	43.95	4.76	35.00	2-126	41	a,b
Komodo	Sebita	88.57	300.60	135.00	66.00	0-3987	35	a,b
Komodo	Wau	100	44.40	7.86	38.00	6-104	15	a,b
Nusa Kode	Kode	100	91.86	8.63	90.00	59-131	7	b
Rinca	Baru	94.44	43.33	6.50	27.50	0-150	36	a
Rinca	Buaya	100	42.39	4.26	39.00	12-102	31	a,b
Rinca	Dasami	100	33.29	3.08	32.50	5-63	24	a
Rinca	Tongkir	100	66.74	10.75	49.00	14-249	31	a,b
Gili Motang	Motang	100	26.50	3.75	25.50	6-60	18	a

by the presence of three lizards harbouring 1748, 2362, 3987 ticks, respectively. Hence the median value for this population was calculated to be 66 ticks / lizard.

Comparison of the mean interannual tick prevalence and abundance for lizard hosts (N = 37) first captured in 2003 (average tick abundance 33.28 ± 2.35) and again in 2005 (average tick load 31.18 ± 3.85) found no significant difference (Paired t-test: $t_{1, 35}$ = 1.058, P = 0.297). However, for individual hosts there was little concordance between their tick abundance first measured in 2003 and then again in 2005 (R^2= 0.01; ANOVA: $F_{1, 35}$ = 0.59, P = 0.448) suggesting a temporal component to each individual's observed tick load.

2. Relationships between environmental and host dependent variable and tick abundance.

A preliminary analysis (Table 2) indicated that only three of the seven putative covariates were significantly ($P \leq 0.05$) or near significantly ($P \leq 0.1$) positively correlated to tick abundance on Komodo dragons. Lizard body size, body condition and habitat structure were the most influential variables in the candidate covariates and these three variables were retained for further multivariate analysis. Variables that were not significantly related to tick abundance included: island area, host population density,

Table 2. Linear and non-linear regression models assessing univariate relationships between putative covariates and tick abundance log (x +1) on Komodo dragons. Covariates with P ≤ 0.1 were retained for further multivariate analysis.

| Covariate	Equation	R^2	F	Df	P
	Univariate Model Summary				
1. Body Length (SVL)	Linear	0.061	15.252	1,236	<0.001
	Quadratic	0.209	31.060	2,235	<0.001
	Cubic	0.215	21.337	3,234	<0.001
2. Body Condition	Linear	0.123	32.970	1,236	<0.001
	Quadratic	0.199	29.248	2,235	<0.001
	Cubic	0.206	20.277	3,234	<0.001
3. Habitat	Linear	0.011	2.660	1,236	0.100
	Quadratic	0.012	1.458	2,235	0.235
	Cubic	0.012	1.457	3,234	0.235
4. Inbreeding coefficient	Linear	0.001	0.231	1,236	0.631
	Quadratic	0.018	2.141	2,235	0.120
	Cubic	0.018	2.148	3,234	0.119
5. Host population density	Linear	0.008	1.800	1,236	0.181
	Quadratic	0.008	0.949	2,235	0.389
	Cubic	0.008	0.938	3,234	0.393
6. Sampling time	Linear	0.001	0.210	1,236	0.647
	Quadratic	0.004	0.445	2,235	0.642
	Cubic	0.004	0.413	3,234	0.662
7. Island area	Linear	0.004	0.836	1,236	0.361
	Quadratic	0.005	0.585	2,235	0.558
	Cubic	0.005	0.582	3,234	0.560

host population inbreeding coefficients and sampling time. These variables were not included in subsequent generalized linear modelling.

Multiple models were tested via generalized linear modelling to estimate to what degree body size, body condition, habitat diversity and their interactions, were associated with variation in tick abundance on Komodo dragons. Six models (Table 3) were considered with a model incorporating body size, body condition (cubic function) and their respective interactions with habitat diversity being positively correlated with tick abundance on Komodo dragons (Figure 4). This model exhibited the strongest model support with w_i approaching 53% support. Further, this model accounted for 23.10% of the variation in tick abundance on Komodo dragons. Additional unmeasured covariates contribute to the unaccounted for variation in tick abundance among Komodo dragons.

Table 3. Descending rank of models estimated using generalized linear modelling to evaluate the relationship between environmental and host dependent variables and tick abundance on Komodo dragons (N = 238). Models are ranked by Akaike Information Criteria (AIC), the difference between model support is denoted by delta AIC and the level of support for each model is described by w_i. For the most parsimonious model the adjusted coefficient of determination (R^2_{adj}) is presented. Independent and dependent variables are abbreviated as follows: tick abundance log(x+1) = logtic; body length = SVL; body condition = bcon; habitat diversity = hab. Superscripts denote non-linear terms (2 = quadratic and 3 = cubic) and asterisks denote interactions between terms.

| Model	AIC	$\varDelta$AIC	w_i	R^2_{adj}
logtic= svl + bcon^3 + svl*bcon + svl*hab + hab*bcon	258.23	0.00	0.53	0.231
logtic = svl + hab + bcon^3 + svl*bcon + svl*hab + bcon*hab	259.45	1.22	0.29	
logtic = svl + bcon + hab + bcon^3 + svl*bcon + svl*hab + bcon*hab	261.22	2.97	0.12	
logtic = svl + bcon + hab + svl^2 + bcon^3 + svl*bcon + svl*hab + bcon*hab	263.28	5.05	0.04	
logtic = svl + bcon + hab + svl^2 + bcon^3 + svl*bcon + svl*hab + bcon*hab+svl*bcon*hab	266.11	7.88	0.01	
logtic = svl	303.09	44.86	0.00	
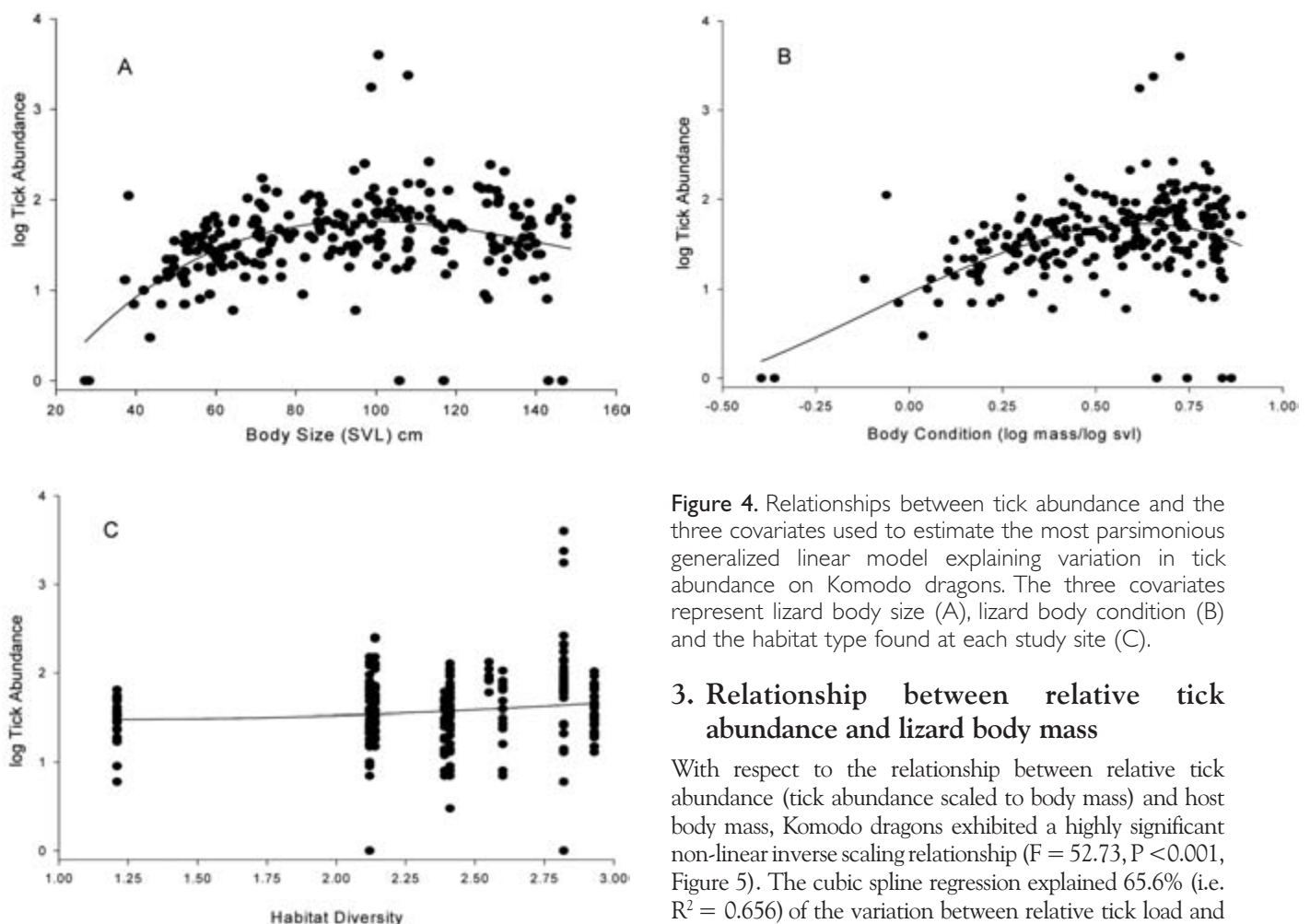
Figure 4. Relationships between tick abundance and the three covariates used to estimate the most parsimonious generalized linear model explaining variation in tick abundance on Komodo dragons. The three covariates represent lizard body size (A), lizard body condition (B) and the habitat type found at each study site (C).

3. Relationship between relative tick abundance and lizard body mass

With respect to the relationship between relative tick abundance (tick abundance scaled to body mass) and host body mass, Komodo dragons exhibited a highly significant non-linear inverse scaling relationship (F = 52.73, P <0.001, Figure 5). The cubic spline regression explained 65.6% (i.e. $R^2 = 0.656$) of the variation between relative tick load and
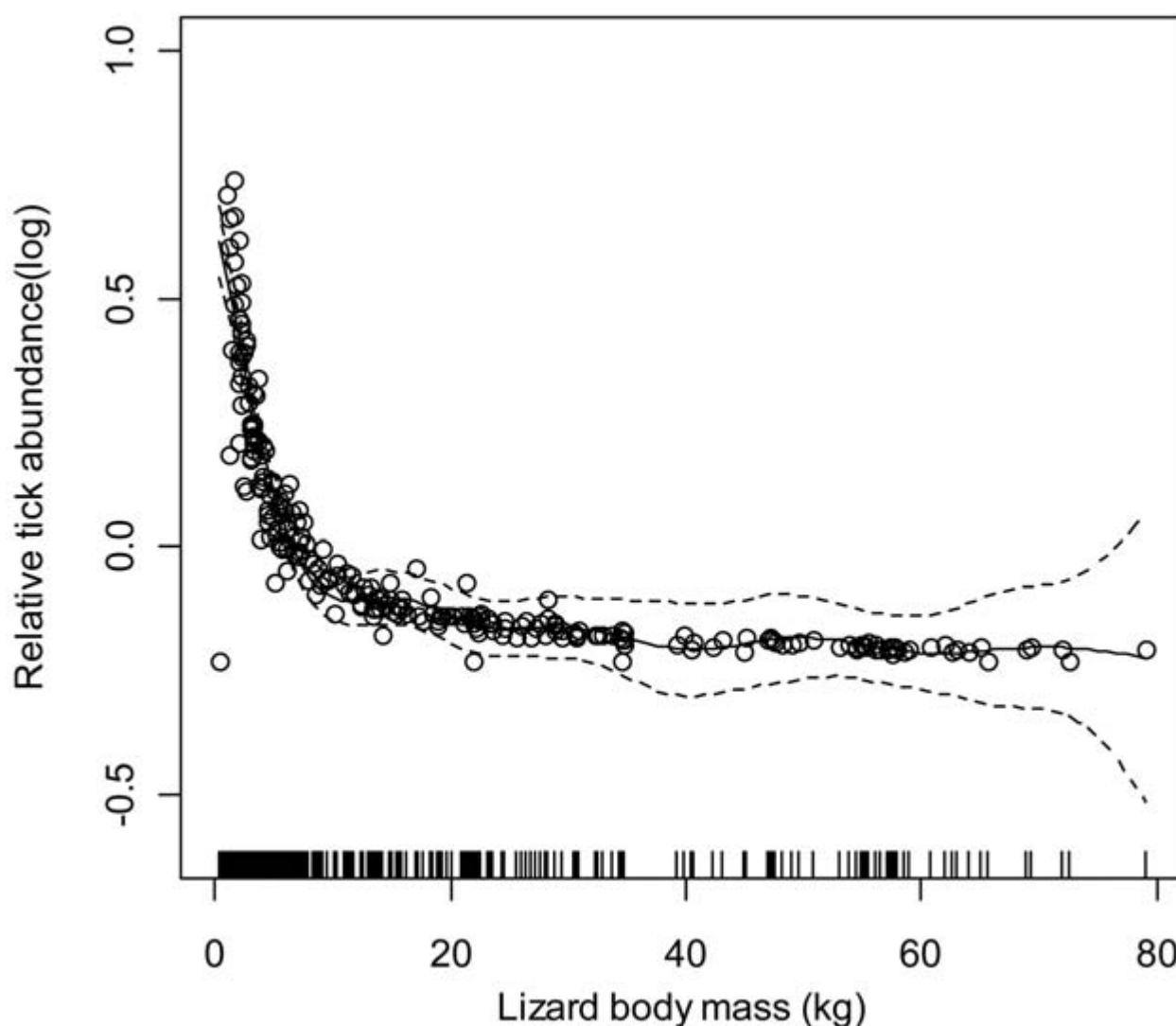
Figure 5. The graphical summary of GAM model fit between lizard body mass and relative tick abundance. Relative tick abundance is a standardized measure representing the quotient of log tick abundance and body mass. The solid curve is the cubic smoothing spline fit for body mass and the dashed curves are the point wise 95% credible intervals around the fit.

lizard body mass. In effect, as lizards increased in body mass their relative tick load decreased exponentially until they reached a body mass of about 10kg. Above 10 kg the relative tick abundance on Komodo dragons was very low and largely invariant with further increases in body mass.

4. Relationships between host somatic growth and tick abundance.

The interactions between an individual's tick abundance and somatic growth are presented as non-linear models (Table 4). There was no significant relationship between tick load and somatic growth in any island population.

Discussion

Komodo dragons studied at nine sites across four islands exhibited a uniformly high prevalence of ticks, with ≈ 98 % of all dragons being parasitised. Most lizards hosted low numbers of ticks (<40), however ≈ 1% of individual lizards sampled had tick abundances almost two orders of magnitude greater (i.e. up to 3987 ticks on a single lizard). The mean tick abundance among lizard populations was significantly different but was unrelated to either genetic similarities or geographic proximities among host populations. It thus appears that each host population is following its own local trajectory for its

Table 4. The relationship between tick abundance and somatic growth rates of Komodo dragons inhabiting four islands.

Island	Model	R	df	F	P
Komodo	growth = 0.055+-0.352*lnTL+0.209*lnTL^2+-0.031*lnTL^3	0.234	3,32	0.619	0.602
Rinca	growth = 0.147+-0.153*lnTL+0.0345*lnTL^2	0.145	2,59	0.638	0.532
Gili Motang	growth = = 0.602-2.675*lnTL+ 2.116*lnTL^2+ -0.463*lnTL^3	0.546	3,6,	0.8503	0.515
Nusa Kode	insufficient data (1 recapture only in 2004)	-	-	-	-

parasite dynamics. This may be a reflection of unique adaptations of either host or parasite populations that influence the parasite composition and demography of a population, or perhaps a reflection of the different parasite lineages that are parasitising Komodo dragons at different locales within and among islands. Individual parasite lineages have been found to show considerable geographic structure among islands and among host species in a study on avian malaria in passerine birds of the Lesser Antilles (Fallon *et al.* 2003). In archipelagos, where populations may be distributed across several islands, evolutionary and ecological processes may differ and can greatly influence intraspecific divergence across relatively small geographic scales.

We were able to explain 23% of the variation in tick abundance on Komodo dragons. Three variables: body size, body condition and their interactions with habitat were positively correlated with tick abundance. Larger and better-conditioned hosts were more likely to have higher tick burdens than smaller and / or poorer conditioned lizards. However, it was evident that as lizards increased in both body size and body condition the number of ticks carried reached an asymptote and even declined for the largest lizards. These relationships appear similar to a type 2 response observed in age-specific host-parasite interactions (Wilson *et al.* 2002). Such responses are expected to occur when parasite acquisition and mortality / loss are constant, so that the average number of parasites per host will increase towards an asymptote determined by the balance between these two rates (Wilson *et al.* 2002). In our study, animals above 140 cm snout to vent length are all adult males and these animals exhibited relatively low tick burdens, suggestive of sex mediated differences in this species. The decreased rate of tick acquisition in larger lizards could also arise due to acquired immunity in which hosts, via immunological mechanisms, decrease establishment, survival, reproduction and / or maturation of ticks (Wilson *et al.* 2002). Habitat composition, whilst the least significant of the variables incorporated into the best supporting model, suggested that hosts occupying more complex forest habitat had more ticks relative to lizards in more uniform habitat. Niche partitioning with size could mean that larger animals are using different habitat types relative to smaller conspecifics and so encounter different densities of parasites. Behavioural differences among sex / size classes was found to influence tick load in ball pythons *Python regius*, in which increased movement by adult male pythons, independent of any endocrine mediated immunosupression, was suggested as a factor explaining their higher tick loads relative to other size / sex classes (Aubret *et al.*, 2005).

Many of the variables we considered as putative covariates influencing tick abundance were found not to be important in our study. For example, island area was not correlated with host population tick load. Thus, despite the two large and two small islands being superficially replicated with respect to their environment and ecology, island size was not associated with parasite population parameters. Similarly, the host-population density and levels of population inbreeding among Komodo dragons was not

significantly correlated with an individual's tick load. These results are contradictory to theoretical expectations for relationships between parasite load and host quality, where genetically depauperate hosts have been found to be more susceptible to parasitism than genetically variable hosts (Moritz *et al.* 1991; Cassinello *et al.* 2001; Spielman *et al.* 2004). In fact, the effect of disease or parasitism on novel and often genetically depauperate host populations has been postulated to explain, in part, the increased extinction rate of small isolated island populations relative to mainland populations (van Riper *et al.* 1986; Atkinson *et al.* 1995; Frankham 1998; de Castro and Bolker 2005; Whiteman *et al.* 2006).

In contrast to the positive relationship between body size and tick abundance, relative tick abundance (tick abundance scaled to an individual host's mass) decreased at a non-linear rate up to a weight of 10kg, before essentially asymptoting with increasing mass. Hence larger dragons exhibited relatively lower tick abundances compared to their smaller conspecifics. Irrespective of other mechanisms underpinning body-size related patterns, inverse scaling alone could offer larger dragons decreased costs arising from tick loads. A similar body-size pattern was found in a study by George-Nascimento *et al.* (2004) who looked at endoparasites in 131 species of vertebrate host, and found that both the numbers and the volume of parasites decreased allometrically with host body mass. They concluded that from an evolutionary perspective, large body-size might allow hosts to avoid the deleterious effects of parasitism.

In lizards, the direct costs of ticks have been demonstrated experimentally and include reduced growth, endurance and sprint speeds (Main and Bull 2000; Olsson *et al.* 2000; Uller and Olsson 2004). These effects are thought to influence individual fitness by decreasing survival and / or reproductive effort. However in free-ranging lizard populations the direct costs of ticks are much harder to quantify, so it is difficult to determine the fitness significance of tick infestations. From our study, there was no correlated evidence that ticks are affecting somatic growth, which we assume is an indicator of Komodo dragon fitness. Several mechanisms could account for this relationship. For example, it may be possible that dynamics between parasite and host at the time of this study were relatively benign. Given that ectoparasites should affect their hosts in a density dependent manner, the actual load of ticks, as measured in this study, was comparatively low by large vertebrate standards and could simply be below any threshold to induce fitness costs (Addison, *et al.* 1994). Alternatively, our capacity to determine tick abundance and its relationship with growth rate (or any variable measured in this study) will be influenced by the robustness of our sampling methodology, which was, effectively, single point sampling. It was also evident that while tick abundance at a population level was similar between years, there was no concordance in abundance between years for individual lizards. Hence, to increase the likelihood that we could detect any tick related fitness effects on Komodo dragons, we would need to implement studies designed to measure

host-tick abundance relationships across multiple time periods to account for temporal processes. Alternatively, experimental manipulation (via addition or removal of ticks) could potentially appraise the cost of ticks to their varanid hosts. However both approaches are extremely difficult in the case of Komodo dragons due to the extreme logistical constraints of working on this species. It may be possible, however, to assess the importance of ticks as vectors for blood parasites that are common in some other lizard species (Smallridge

and Bull; 2001). To better understand our results and to identify the effects of ticks on Komodo dragons, we would need to incorporate additional ecological and evolutionary interactions into long-term robust demographic monitoring of both host and tick studies to better determine fine scale interactions. This is essential to increase the likelihood that evidence for any costs of tick infestation to a particular Komodo dragon population is detected and is repeatable under similar demographic or environmental scenarios.

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